



A meta-analysis of recreation effects on vertebrate species richness and abundance

Courtney L. Larson¹ | Sarah E. Reed^{1,2} | Adina M. Merenlender³ | Kevin R. Crooks¹

¹Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado

²Wildlife Conservation Society, Americas Program, Bronx, New York

³Department of Environmental Science, Policy, and Management, University of California, Berkeley, California

Correspondence

Courtney L. Larson, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins CO 80523-1474.
Email: courtney.larson@colostate.edu

Funding information

California Department of Fish and Wildlife, Grant/Award Number: P1582100

Abstract

Most protected areas globally have a dual mission to conserve natural resources and provide access for outdoor recreation or ecotourism, yet questions remain about the ecological effects of recreation. We conducted a global meta-analysis of the effects of recreation on vertebrate richness and abundance. We estimated that vertebrate richness ($n = 15$ articles) and abundance ($n = 32$) are lower in association with higher levels of recreation in over two-thirds (70%) of cases. We observed a moderate negative group-level effect of recreation on bird and mammal abundance, but the group-level effect on fish and reptiles was not significant. Effects were stronger for carnivores and herbivores than for omnivores, and stronger for small-bodied birds and ground-nesting birds than larger and tree- and shrub-nesting birds. Terrestrial activities were associated with reduced vertebrate abundance, whereas aquatic activities were not. Both motorized and nonmotorized activities were associated with reduced vertebrate abundance, but the effect for motorized activities was uncertain due to small sample size. These results pose a challenge to natural resource management agencies who must balance recreation access with natural resource protection, and to conservation organizations that rely on outdoor recreation for public support and funding. We recommend that managers plan recreational access at a regional scale and include some areas that are closed to recreation to minimize trade-offs between recreation and animal conservation.

KEYWORDS

abundance, conservation, meta-analysis, protected areas, recreation, species richness, vertebrates, wildlife

1 | INTRODUCTION

Outdoor recreation is prevalent in protected areas, recently estimated at 8 billion visits per year globally (Balmford et al., 2015). Increasingly, research has demonstrated that recreation can have damaging effects on ecological communities (Larson, Reed, Merenlender, & Crooks, 2016; Monz, Pickering, & Hadwen, 2013; Sato, Wood, & Lindenmayer, 2013). Though recreation may not be the

most severe threat facing global biodiversity, it often occurs in places established to protect species and therefore could have disproportionate impacts. At the same time, nature-based recreation is vital for human health and for building connections with nature that can help foster pro-environmental behaviors (Cooper, Larson, Dayer, Stedman, & Decker, 2015). For these reasons, we must address the challenges recreation poses to protected area management.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. Conservation Science and Practice published by Wiley Periodicals, Inc. on behalf of Society for Conservation Biology

Short-term responses of animals to even quiet recreation can include increased physiological stress (Arlettaz et al., 2007) and time spent in flight and vigilance behaviors (Naylor, Wisdom, & Anthony, 2009). Though habituation to human disturbance can dampen behavioral responses of animals to human presence (Baudains & Lloyd, 2007), it may also increase their vulnerability to predation (Geffroy, Samia, Bessa, & Blumstein, 2015) or conflicts with humans (Bejder, Samuels, Whitehead, Finn, & Allen, 2009). Over time, animals may alter their spatial and temporal habitat use to avoid disturbance (Lesmerises, Déry, Johnson, & St-Laurent, 2018), reducing habitat suitability in areas used by recreationists. Elevated stress, energy expenditures, and shifts in activity patterns at the individual level can scale up and affect population and community measures such as abundance or density (Bötsch, Tablado, & Jenni, 2017), species richness (Reed & Merenlender, 2008), and community composition (Kangas, Luoto, Ihtantola, Tomppo, & Siikamäki, 2010).

However, findings vary widely among individual studies that focus on a single ecosystem, taxon, or type of impact, including some recent studies that have observed limited effects of recreation on animal communities (Kays et al., 2016; Reilly, Tobler, Sonderegger, & Beier, 2017). Accordingly, questions remain about the magnitude of the effects of recreation and their consistency across taxa and scale. A systematic review focused on frequency of recreation effects revealed that although 93% of articles documented at least one effect of recreation on wildlife, there was considerable variation among taxonomic groups and types of activities (Larson et al., 2016).

Meta-analysis is increasingly popular in ecology and conservation as a tool to synthesize evidence across studies and explore large-scale patterns. Meta-analyses can combine data from similar studies to estimate overall effect sizes while considering sources of heterogeneity such as differences in methods or study taxa (Haddaway, 2015). Previous meta-analyses on recreation effects on wildlife have focused on winter recreation (Sato et al., 2013) and behavioral and physiological measures (Bateman & Fleming, 2017). Our analysis complements and builds upon these prior studies by encompassing many types of recreation and focusing on responses at the population and community levels, where decisions about animal conservation and management are typically made. More specifically, we examine differences in vertebrate richness and abundance in response to outdoor recreation. We ask if there are differences among classes of vertebrates, species characteristics, types of recreation, and temporal and spatial patterns of recreational use. Managers of protected areas are increasingly aware of the potential for recreation to impact biodiversity, but little information is available to help them evaluate management options. Examining the findings of individual studies in a synthetic

fashion, we provide broader conclusions about recreation effects that can help inform management decisions to reduce impacts from recreational use of protected areas.

2 | METHODS

2.1 | Article selection

Our search protocol, fully described in Larson et al. (2016), was designed for a high-sensitivity, low-specificity search (Pullin & Stewart, 2006). We used the keywords “tourism” and “recreation” to systematically search for articles published through March 2018 within a list of 196 journals drawn from five Web of Science categories (biodiversity conservation, ecology, zoology, ornithology, and behavioral sciences; Table S1 in Data S1). Since we relied on the journal category feature within Web of Science to narrow the scope of our search, we did not replicate the search in additional databases or gray literature. We screened titles and abstracts to remove clearly irrelevant articles, then reviewed full-text articles and selected those that met the following inclusion criteria: (a) articles estimated species richness and/or abundance of at least one animal species; (b) articles reported species richness and/or abundance estimates at two or more categorical levels of nonconsumptive recreation while other site characteristics were similar; (c) articles included sufficient data (in results, figures, or supplemental materials) to calculate effect sizes (Figure 1). We define “abundance” to include indices of relative abundance or activity levels, such as detection frequencies of animals or sign. The second criterion ensured that studies had similar designs that compared recreation effects between categorical levels of use (e.g., sites with relatively low and high levels of recreation), while other site characteristics (e.g., habitat, geographic location) did not differ substantially (as assumed or measured by the study authors). While studies measuring recreation as a continuous variable are useful for understanding effects of recreation, they were difficult to include in meta-analyses because authors frequently analyzed such data with multivariate models (i.e., recreation variables along with covariates), meaning that the reported effect of recreation was conditional on the effects of covariates. We therefore excluded these studies from our analysis. The second criterion also filtered out studies examining consumptive forms of recreation such as hunting, fishing, and collecting.

2.2 | Data extraction

We extracted pairs of estimates (“comparisons”) of vertebrate richness or abundance at low and high levels of recreation from each included article. Many articles contained data for multiple species or temporal and spatial scales, which we

FIGURE 1 PRISMA flow diagram showing the number of articles that were located, retained, and excluded at each stage of the meta-analysis process

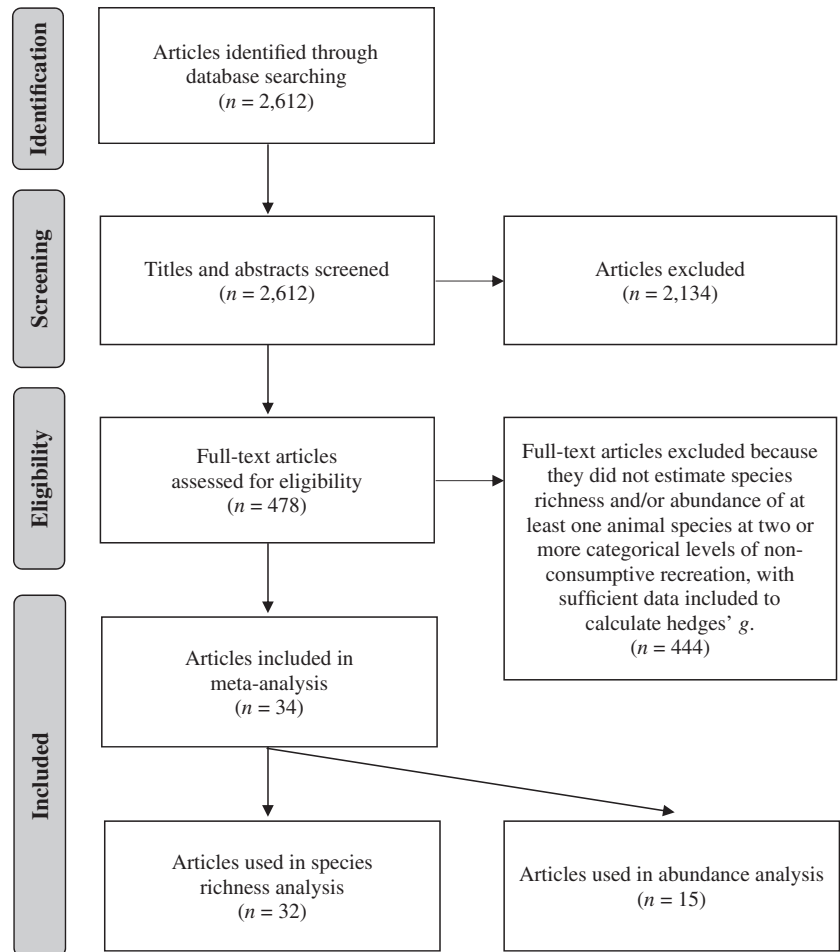


TABLE 1 Covariates extracted from the included studies

Variable	Description or list of categories
Taxonomic group	Amphibian, bird, fish, mammal, reptile
Species	
Recreation substrate	Aquatic, winter, terrestrial
Recreation motorized	Motorized, nonmotorized
Response variable	Species richness, abundance
Comparison type	Spatial, temporal
Disturbance type	Novel, ongoing
Body mass ^a	Average body mass (g)
Diet ^a	Carnivore, omnivore, herbivore
Nesting behavior ^a	Ground-nesting, shrub-nesting, tree-nesting

^aSources: Jones et al. (2009); Parr et al. (2014); Cornell Lab of Ornithology (2018); Myers et al. (2018).

retained as separate comparisons in the database. For each comparison, we recorded the focal taxa, type of recreation activity (aquatic, winter, or terrestrial; motorized or non-motorized), and type of response variable (species richness or abundance; Table 1). We recorded whether the recreation disturbance was a temporal difference, defined as a comparison

between recreation levels at the same site(s) at different times, or a spatial difference, defined as a comparison between recreation levels at different sites at the same time. We categorized the recreation disturbance as “novel” to the study system if it differed from the baseline recreation level based on the authors' descriptions (e.g., an experimental hiking treatment in a forest closed to recreation); otherwise, the disturbance was labeled “ongoing.” From external databases, we collected the average body mass, diet category, and nesting behavior (for birds) of each species (Cornell Lab of Ornithology, 2018; Jones et al., 2009; Myers et al., 2018; Parr et al., 2014). We then extracted the means, standard deviations, and sample sizes of species richness or abundance estimates at low and high-recreation levels from the text, supplemental materials, or figures using an online digitization tool (Rohatgi, 2017). We used data from the lowest taxonomic grouping available.

We pooled data to increase consistency among articles, including species richness and abundance estimates from individual study sites or sampling seasons within each article. When measurements were taken multiple times before or after a recreation “treatment” ($n = 1$ article), we used only the time points closest to the treatment to increase similarity among comparisons. Likewise, when articles ($n = 2$) tested

three or more levels of recreation (e.g., no, low-, and high-recreation sites), we used data from the lowest and highest impact sites. Finally, we pooled estimates from population segments such as age class or sex.

2.3 | Statistical methods

For each comparison, we calculated hedges' g and its variance, a standardized difference of means commonly used as an effect size in meta-analysis (Koricheva, Gurevitch, & Mengersen, 2013). We used means and standard deviations when available; otherwise we converted test statistics such as χ^2 or F -statistics to hedges' g . The units of g are standard deviations separating the means of the low- and high-recreation groups. Negative values of g indicate that vertebrate richness or abundance was greater with lower levels of recreation, and positive values mean that richness or abundance was greater with higher levels of recreation. We consider absolute values of $g \geq .8$ a large effect, $.5$ a moderate effect, and $.2$ a small effect (Cohen, 1988). A hypothetical example in which a mean of 12 (SD = 3) species were observed at 10 sites with recreation and 14 (SD = 3) species were observed at 10 sites without recreation would result in $g = -.64$, a moderate negative effect. Confidence intervals (95%) accompany all hedges' g values; if these do not include zero, we conclude that the means of low- and high-recreation estimates are significantly different.

We built multi-level mixed-effects models (Nakagawa & Santos, 2012) for richness and abundance to calculate the pooled effect size across all included studies, using the R package *metafor* (Viechtbauer, 2010). In each model we included a random effect for article, because some articles contributed multiple data points from the same location and investigator team, and for species since we expected effects of recreation to differ among species. Effect sizes were weighted by inverse variances in all models (Koricheva et al., 2013). We did not separately model relative abundance measures (detections of animals or sign; $n = 88$) from estimates derived from mark-recapture analyses ($n = 6$) or from complete censuses of territories ($n = 4$) because preliminary analysis showed little difference in pooled effect sizes among these measures. We then built models to explore how effect size varied with the following covariates: broad taxonomic group, recreation activity categories, novel or ongoing disturbance, recreation disturbance type (spatial or temporal), body mass, diet, and nesting location. We present hedges' g estimates for each level of categorical covariates and regression coefficients ($\beta \pm SE$) for continuous covariates. To assess publication bias, which occurs when studies with statistically significant results are more likely to be published than those without (Nakagawa & Santos, 2012), we visually inspected funnel plots and used Egger's regression to examine correlations

between effect size and sampling variance (Egger, Davey Smith, Schneider, & Minder, 1997). To assess our ability to detect effects of varying magnitudes, we conducted a retrospective power analysis using the mean sample sizes, effect sizes, and effect size variances from the included studies (Valentine, Pigott, & Rothstein, 2010).

3 | RESULTS

Our inclusion criteria filtered the initial list of 2,612 articles down to 34, yielding 20 species richness comparisons and 103 abundance comparisons (Tables S2 and S3 in Data S2). Birds were well-represented, with 45 comparisons (37% of 123 total) on 20 species from 15 articles (44% of 34 total). There were a similar number of comparisons for fish (47, or 38% of total) on more species (28), but from fewer articles (6, or 18% of total). Mammals had 27 comparisons (22% of total) on 16 species from 10 articles (29% of total). Reptiles were poorly represented, with four comparisons (3% of total) on three species from four articles (12% of total). There were no articles on amphibians included in the dataset. Across all comparisons for which diet type could be specified, 70% measured responses of carnivores or insectivores, 17% omnivores, and 13% herbivores. For bird comparisons for which nesting behavior could be specified, 50% measured responses of tree-nesters, 42% ground-nesters, and 8% shrub-nesters. Most comparisons assessed responses to terrestrial (59%) or aquatic (38%) recreation activities, with few (2%) assessing responses to winter recreation. Nearly all comparisons focused on non-motorized (97%) rather than motorized (3%) recreation. Most comparisons were spatial (83%) rather than temporal (17%) and investigated recreation disturbance that was ongoing (87%) rather than novel (13%).

We found a moderate negative effect of recreation on vertebrate richness (hedges' g [95% CI] = -0.58 [-1.01 , -0.15]; Figure 2a) and a small to moderate negative effect on abundance (-0.45 [-0.72 , -0.18]; Figure 2b). Retrospective power analysis showed that we could detect a moderate effect on richness with power of 0.64 and on abundance with power of 0.77. Egger's regressions were nonsignificant, suggesting little evidence of publication bias (richness: $z = -1.62$, $p = .1$; abundance: $z = -0.73$, $p = .47$).

3.1 | Taxonomic differences and species traits

Effect sizes were large and negative for bird (-0.89 [-1.5 , -0.28]; Figure 2a) and mammal (-0.88 [-1.78 , 0.01]) richness. Fish richness was similar at low- and high-recreation levels (-0.02 [-0.69 , 0.66]). Insufficient data precluded separate analyses of differences in reptile richness. We observed a moderate negative effect of recreation on bird (-0.58 [-0.97 , -0.19]; Figure 2b) and mammal (-0.74 [-1.22 ,

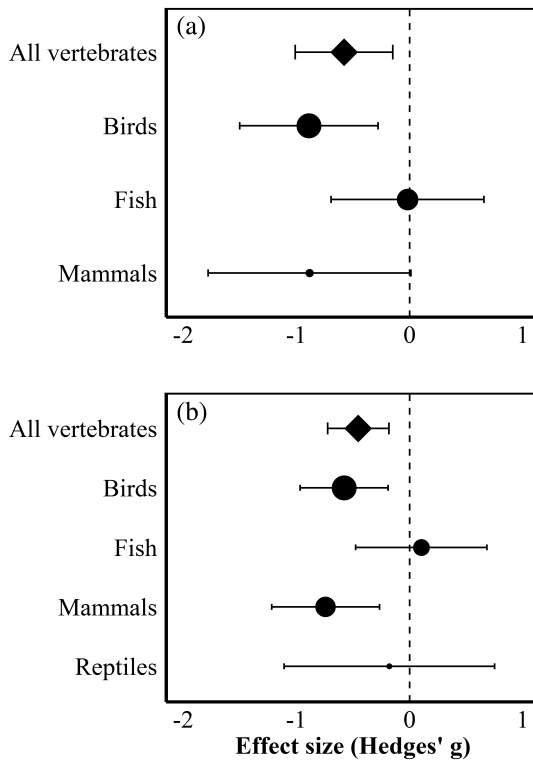


FIGURE 2 Effect sizes comparing differences in (a) species richness and (b) abundance between low- and high-recreation levels, broken down into broad taxonomic groups. The dot size is proportional to the sample size in each group (the size of the diamond is not meaningful for the “all vertebrates” group). Error bars show 95% confidence intervals

–0.27]) abundance, but no differences in fish (0.1 [–0.48, 0.68]) or reptile (–0.18 [–1.11, 0.75]) abundance between recreation levels.

Bird body mass was positively related to hedges' *g* for abundance, meaning that small bird abundance was more strongly reduced in association with high recreation than the abundance of larger birds ($\beta \pm SE = 0.36 \pm 0.17$, $p = .04$). There was no relationship between mammal body mass and hedges' *g* for abundance ($\beta \pm SE = -0.08 \pm 0.09$, $p = .41$). We observed a moderate negative effect of recreation on carnivore (–0.67 [–1.01, –0.33]) and herbivore (–0.72 [–1.21, –0.23]) abundance, while omnivore abundance (–0.07 [–0.52, 0.38]; Figure 3a) did not differ between high and low levels of recreation. The difference in abundance was especially pronounced for carnivorous birds (–0.79 [–1.32, –0.26]) and mammals (–0.84 [–1.39, –0.28]), whereas the confidence interval of every other combination of diet and taxonomic group included zero. The abundance of ground-nesting birds was lower when recreation was higher (moderate effect size of –0.64 [–1.21, –0.07]), whereas tree-nesting (–0.36 [–0.94, 0.21]) and shrub-nesting (–0.36 [–1.47, 0.75]) bird abundance was reduced, but not significantly (Figure 3b).

3.2 | Recreation types and timing

We observed a large negative effect of terrestrial recreation on vertebrate richness (–0.88 [–1.37, –0.4]) and a moderate negative effect on abundance (–0.61 [–0.91, –0.31]; Figure 3c), but no effect of aquatic recreation (richness: –0.01 [–0.66, 0.64]; abundance: 0.1 [–0.46, 0.66]). We detected a small to moderate negative effect of nonmotorized recreation on vertebrate abundance (–0.46 [–0.75, –0.18]) whereas the effect of motorized recreation was not significantly different from zero (–0.35 [–1.38, 0.67]; Figure 3d). Studies of temporal differences in recreation levels (richness: –1.08 [–2.06, –0.09]; abundance: –0.67 [–1.21, –0.12]) reported larger negative effect sizes than did studies of spatial differences (richness: –0.46 [–0.94, 0.01]; abundance: –0.38 [–0.71, –0.06]; Figure 3e). Both vertebrate richness and abundance were lower in association with novel disturbances (richness: –1.23 [–1.99, –0.47]; abundance: –0.55 [–1.06, –0.04]) than with ongoing disturbances (richness: –0.48 [–0.94, –0.01]; abundance: –0.43 [–0.73, –0.14]; Figure 3f).

4 | DISCUSSION

Across many vertebrate species, species richness and abundance were lower in association with higher levels of recreation. Differences in vertebrate richness and abundance were approximately half a standard deviation between high and low recreation levels. This means that in approximately 7 out of 10 comparisons, vertebrate richness or abundance is expected to be lower with higher levels of recreation.

Despite substantial knowledge gaps and high variability in wildlife responses to recreation, we identified some traits that may indicate sensitivity to recreation. Bird and mammal richness and abundance were reduced in association with higher levels of recreation whereas fish richness and abundance and reptile abundance were not. However, the near-zero effect sizes for fish and reptiles may be due in part to differential responses to ecotourism operations that involve supplemental feeding. When analyzed separately, recreation involving feeding had a slight positive effect size for fish abundance (0.09 [–0.31, 0.48]) and richness (0.19 [–0.78, 1.16]) whereas recreation without feeding had a slight negative effect size for abundance (–0.11 [–0.46, 0.23]) and a moderately strong negative effect size for richness (–0.67 [–2.25, 0.93]), though all the estimates were imprecise. Just one study involved supplemental feeding of reptiles (Iverson, Converse, Smith, & Valiulis, 2006), but when abundance models were run excluding this study, the effect size for reptile abundance was large and negative (–0.81 [–1.92, 0.30]). The change in effect size when this comparison was removed also highlights how limited literature in

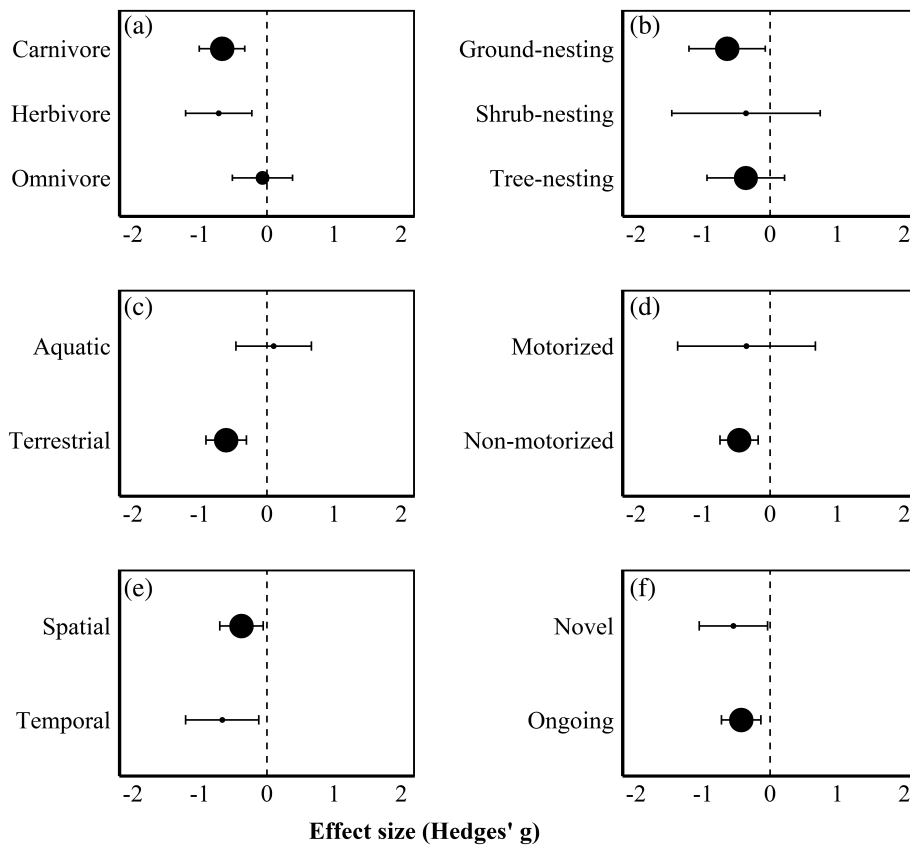


FIGURE 3 Effect sizes comparing differences in abundance between low-recreation and high-recreation levels, broken down by (a) diet type, (b) nesting behavior (birds only), (c) aquatic or terrestrial activities, (d) motorized or nonmotorized activities, (e) spatial or temporal comparison of recreation levels, and (f) novel or ongoing disturbance from recreation. The dot size is proportional to the sample size in each group. Error bars show 95% confidence intervals

certain subgroups, such as reptiles, limits inference regarding recreation impacts.

Carnivore and herbivore abundances were reduced in high-recreation areas more often than omnivore abundance; this effect was even stronger for avian and mammalian carnivores. Dietary and habitat generalists are known to be more human-tolerant than specialists (Devictor, Julliard, & Jiguet, 2008) so it is logical that omnivores would be less sensitive; however, we were not able to examine differences among species with narrow or broad diets within these general categories. For birds, the abundance of small-bodied and ground-nesting species was more frequently reduced with high recreation levels than the abundance of larger-bodied and tree- and shrub-nesting species. This finding is consistent with Samia, Nakagawa, Nomura, Rangel, and Blumstein (2015), who found that smaller birds had reduced tolerance of people compared to larger birds, perhaps because larger animals are more likely to become tolerant to reduce costs associated with regular disturbance. However, our dataset did not include studies on the abundance of raptors, some of which respond strongly to human disturbance (Spaul & Heath, 2016).

Impacts of recreation differed among types of recreational activities. Terrestrial recreation had stronger effects on vertebrate richness and abundance than aquatic recreation. Though just two studies in our analysis examined winter recreation,

the authors observed dramatically lower animal densities in areas with recreation (Seip, Johnson, & Watts, 2007; Slauson, Zielinski, & Schwartz, 2017). Furthermore, our results imply that nonmotorized activities can affect vertebrate abundance just as strongly as motorized recreation, though the small sample size for motorized activities ($n = 4$ articles) suggests that this finding should be considered preliminary. Previous research shows that nonmotorized recreation may have more frequent impacts on wildlife (Larson et al., 2016) and it can interact with motorized recreation to facilitate increased disturbance by pedestrians (Spaul & Heath, 2016).

Reductions in vertebrate abundance were greater for temporal than for spatial comparisons. Long-term temporal comparisons (multiple years at each level of recreation, $n = 3$) had the greatest effect sizes, perhaps suggesting that repeated human disturbance can have cumulative effects. However, novel disturbances had a stronger effect than ongoing disturbances, suggesting that in some contexts, habituation to recreation may occur. Findings from studies focused on habituation to recreation have been mixed, with some finding evidence for habituation (e.g., Baudains & Lloyd, 2007; Ellenberg, Mattern, & Seddon, 2009) and others finding little (e.g., Constantine, Brunton, & Dennis, 2004; Neumann, Ericsson, & Dettki, 2010). The apparent contradiction in our results echoes the variability of wildlife responses to recreation documented in the literature; it is not

yet clear under which circumstances (e.g., species, landscape factors, intensity of recreational use) recreation effects accumulate or attenuate over time and space, but there is some evidence that habituation potential depends on body size, sex, and temperament of individual animals (e.g., boldness; Ellenberg et al., 2009; Samia et al., 2015). Furthermore, very short temporary disturbances (≤ 1 day) are rarely studied ($n = 2$) despite the increasing popularity of adventure racing and other high-intensity, short-term events inside protected areas (Newsome, 2014).

The shape of the wildlife response curve as recreational use increases remains an open question (Monz et al., 2013). Our low- and high-recreation categories spanned a wide range of intensities and were relative within studies rather than absolute measures. The large variation in how recreation levels were measured and reported meant we were unable to reclassify and standardize levels across articles or satisfactorily categorize the spatial scale of the recreation comparison. Future studies should provide clear empirical estimates of recreation levels at all study locations to aid comparisons across studies and allow identification of thresholds of recreational use at which effects become more severe. Furthermore, we encourage the publication of full results for all species and population segments measured in the study, including those with nonsignificant results, to help assess sensitivity within and among animal taxa.

Our findings show that recreation has an overall negative effect on vertebrate species richness and abundance. Despite variability in animal responses to recreation and remaining knowledge gaps, we believe our findings underline the importance of managing recreation on conservation lands. The trade-offs between recreation and conservation pose a problem for conservation organizations and natural resource managers, given participation in outdoor recreation has been linked to interest in conservation easements (Farmer, Brenner, Drescher, Dickinson, & Knackmuhs, 2016), financial contributions to conservation organizations (Zaradic, Pergams, & Kareiva, 2009), and pro-conservation behaviors (Cooper et al., 2015). Funding sources for land acquisition (e.g., the U.S. Land and Water Conservation Fund) often mandate public access, limiting managers' ability to restrict recreation for conservation objectives. While publicly-owned protected areas are the cornerstone of global conservation efforts, an estimated 94% of them are open to recreation (Eagles et al., 2002; IUCN & UNEP, 2014). This includes the strictest IUCN categories (1a and 1b), which allow "non-intrusive" recreation (Dudley, 2008), although the types and intensities of recreation considered to be nonintrusive is not specified.

Despite the need to manage recreation, management agencies rarely have enough resources to adequately monitor recreational use given considerable spatial and temporal

variability in visitation (Cessford & Muhar, 2003; Larson, Reed, Merenlender, & Crooks, 2018). Thus, even if researchers had a clear understanding of threshold levels of recreational use that result in negative outcomes for wildlife, managers may struggle to ascertain where or when recreational limits are exceeded. Public opposition to trail closures, caps on daily visitation, or reservation systems can be strong and could damage the support for conservation agencies and organizations. Therefore, we believe that the best option to minimize trade-offs between recreation and species conservation is to maintain some areas that are closed to recreation. If planning for recreational access is done at the regional level, managers could ensure that protected area networks include some areas that are closed to recreation, balancing the dual land uses of conservation and recreation at the scale of the protected area network instead of each individual protected area.

ACKNOWLEDGMENTS

C.L.L. is supported by a State Wildlife Grant from the California Department of Fish and Wildlife. We thank Richard Knight, Larissa Bailey, Dan Blumstein, and an anonymous reviewer for helpful comments on the manuscript. The final dataset is available in Supplemental Information (Tables S2 and S3 in Data S2).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

C.L.L., S.E.R., A.M.M., and K.R.C. conceived the ideas for the study. S.E.R. acquired funding that supported the study. C.L.L. collected and analyzed data and wrote the first draft of the manuscript. All authors revised and edited the manuscript and approved publication.

ETHICS STATEMENT

The study did not require approval.

ORCID

Courtney L. Larson  <https://orcid.org/0000-0003-3878-259X>

Adina M. Merenlender  <https://orcid.org/0000-0002-0681-8642>

REFERENCES

- Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., & Jenni-Eiermann, S. (2007). Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proceedings: Biological Sciences*, *274*, 1219–1224.
- Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., ... Manica, A. (2015). Walk on the wild side: Estimating the global magnitude of visits to protected areas. *PLoS Biology*, *13*, e1002074.
- Bateman, P. W., & Fleming, P. A. (2017). Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biological Conservation*, *211*(Part A), 10–19.
- Baudains, T. P., & Lloyd, P. (2007). Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation*, *10*, 400–407.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, *395*, 177–185.
- Bötsch, Y., Tablado, Z., & Jenni, L. (2017). Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B*, *284*, 20170846.
- Cessford, G., & Muhar, A. (2003). Monitoring options for visitor numbers in national parks and natural areas. *Journal for Nature Conservation*, *11*, 240–250.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). New York, NY: Lawrence Erlbaum Associates.
- Constantine, R., Brunton, D. H., & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behavior. *Biological Conservation*, *117*, 299–307.
- Cooper, C., Larson, L., Dayer, A., Stedman, R., & Decker, D. (2015). Are wildlife recreationists conservationists? Linking hunting, birdwatching, and pro-environmental behavior. *The Journal of Wildlife Management*, *79*, 446–457.
- Cornell Lab of Ornithology. (2018). *All About Birds* (online). Ithaca, NY: Cornell University. Retrieved from <https://www.allaboutbirds.org>
- Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, *117*, 507–514.
- Dudley, N. (Ed.). (2008). *Guidelines for applying protected area management categories*. Gland, Switzerland: IUCN.
- Eagles, P. F. J., McCool, S. F., Haynes, C. D., & United Nations Environment Programme, World Tourism Organization & International Union for Conservation of Nature and Natural Resources. (2002). *Sustainable tourism in protected areas: Guidelines for planning and management*. Gland, Switzerland: IUCN–the World Conservation Union.
- Egger, M., Davey Smith, G., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ (Clinical Research ed.)*, *315*, 629–634.
- Ellenberg, U., Mattem, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behavior*, *77*, 289–296.
- Farmer, J. R., Brenner, J. C., Drescher, M., Dickinson, S. L., & Knackmuhs, E. G. (2016). Perpetual private land conservation: The case for outdoor recreation and functional leisure. *Ecology and Society*, *21*(2), 46.
- Geffroy, B., Samia, D. S., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, *30*, 755–765.
- Haddaway, N. R. (2015). A call for better reporting of conservation research data for use in meta-analyses. *Conservation Biology*, *29*, 1242–1245.
- IUCN & UNEP. (2014). *The world database on protected areas (WDPA)*. Cambridge, UK: UNEP-WCMC.
- Iverson, J. B., Converse, S. J., Smith, G. R., & Valiulis, J. M. (2006). Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cyclura inornata*): Human disturbance and density-dependent effects. *Biological Conservation*, *132*, 300–310.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*(9), 2648.
- Kangas, K., Luoto, M., Ihantola, A., Tomppo, E., & Siikamäki, P. (2010). Recreation-induced changes in boreal bird communities in protected areas. *Ecological Applications*, *20*, 1775–1786.
- Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., ... McShea, W. J. (2016). Does hunting or hiking affect wildlife communities in protected areas? *Journal of Applied Ecology*, *54*, 242–252.
- Koricheva, J., Gurevitch, J., & Mengersen, K. (Eds.). (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton, NJ: Princeton University Press.
- Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One*, *11*, e0167259.
- Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2018). Accessibility drives species exposure to recreation in a fragmented urban reserve network. *Landscape and Urban Planning*, *175*, 62–71.
- Lesmerises, F., Déry, F., Johnson, C. J., & St-Laurent, M.-H. (2018). Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. *Biological Conservation*, *217*, 149–156.
- Monz, C. A., Pickering, C. M., & Hadwen, W. L. (2013). Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. *Frontiers in Ecology and the Environment*, *11*, 441–446.
- Myers, P., Espinosa, R., Parr, C., Jones, T., Hammond, G., & Dewey, T. (2018). *The animal diversity web* (online). Ann Arbor, MI: University of Michigan. Retrieved from <https://animaldiversity.org>
- Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, *26*, 1253–1274.
- Naylor, L. M., Wisdom, M. J., & Anthony, R. G. (2009). Behavioral responses of north American elk to recreational activity. *Journal of Wildlife Management*, *73*, 328–338.
- Neumann, W., Ericsson, G., & Dettki, H. (2010). Does off-trail backcountry skiing disturb moose? *European Journal of Wildlife Research*, *56*, 513–518.
- Newsome, D. (2014). Appropriate policy development and research needs in response to adventure racing in protected areas. *Biological Conservation*, *171*, 259–269.
- Parr, C. S., Wilson, N., Leary, P., Schulz, K. S., Lans, K., Walley, L., ... Conrigan, R. J., Jr. (2014). The encyclopedia of life v2: Providing global access to knowledge about life on earth. *Biodiversity Data Journal*, *2*, e1079.

- Pullin, A. S., & Stewart, G. B. (2006). Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, 20, 1647–1656.
- Reed, S. E., & Merenlender, A. M. (2008). Quiet, nonconsumptive recreation reduces protected area effectiveness. *Conservation Letters*, 1, 146–154.
- Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation*, 207, 117–126.
- Rohatgi, A. (2017). WebPlotDigitizer. Retrieved from <http://arohatgi.info/WebPlotDigitizer>.
- Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6, 8877.
- Sato, C. F., Wood, J. T., & Lindenmayer, D. B. (2013). The effects of winter recreation on alpine and subalpine fauna: A systematic review and meta-analysis. *PLoS One*, 8, e64282.
- Seip, D. R., Johnson, C. J., & Watts, G. S. (2007). Displacement of mountain Caribou from winter habitat by snowmobiles. *Journal of Wildlife Management*, 71, 1539–1544.
- Slauson, K. M., Zielinski, W. J., & Schwartz, M. K. (2017). Ski areas affect Pacific marten movement, habitat use, and density. *The Journal of Wildlife Management*, 81, 892–904.
- Spaul, R. J., & Heath, J. A. (2016). Nonmotorized recreation and motorized recreation in shrub-steppe habitats affects behavior and reproduction of golden eagles (*Aquila chrysaetos*). *Ecology and Evolution*, 6, 8037–8049.
- Valentine, J. C., Pigott, T. D., & Rothstein, H. R. (2010). How many studies do you need?: A primer on statistical power for meta-analysis. *Journal of Educational and Behavioral Statistics*, 35, 215–247.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.
- Zaradic, P. A., Pergams, O. R. W., & Kareiva, P. (2009). The impact of nature experience on willingness to support conservation. *PLoS One*, 4, e7367.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Larson CL, Reed SE, Merenlender AM, Crooks KR. A meta-analysis of recreation effects on vertebrate species richness and abundance. *Conservation Science and Practice*. 2019; 1:e93. <https://doi.org/10.1111/csp2.93>